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# ON THE RELATIVE ACCEPTABILITY OF THE TYPICAL AND MELANIC MORPHS OF *PANTHEA PALLESCENS* MCDUNNOUGH (LEPIDOPTERA: NOCTUIDAE) TO BIRDS

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*Abstract.*—Typical and melanic individuals of *Panthea pallescens* McDunnough were presented to birds in feeding trials conducted in Leverett, Massachusetts from 1982 to 1985. Both morphs were highly acceptable to the birds, and there were no significant differences between the typicals and melanics with respect to the percentage of specimens taken, the order in which they were taken, the bird species involved, or the behaviors of the birds towards the moths. The data rule out any major difference in the acceptability of the two morphs, but the possibility that melanics might be slightly less acceptable than typicals requires further test.

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Despite an immense literature on "industrial melanism" in moths (see e.g., Kettlewell, 1973; Lees, 1981; Sargent, 1985; Lambert et al., 1986), there have been no reports to my knowledge of the relative acceptability of the typical and melanic morphs of any species exhibiting this phenomenon to avian predators. However, during the course of a long-term study on the relative acceptabilities of over 200 lepidopteran species to birds coming to a feeding tray in Leverett, Massachusetts (Sargent, in prep.), I was able to make such an assessment in the case of *Panthea pallescens* McDunnough.

It seems important to address this question at the present time, as the "classical" explanation of melanism in moths (Kettlewell, 1955, 1956, 1973) has come under increasingly critical scrutiny in recent years (Bishop, 1972; Creed et al., 1973; Sargent, 1974; Bishop and Cook, 1975; Lees and Creed, 1975; Steward, 1977a, b; Lees, 1981; Hailman, 1982; Sermonti and Catastini, 1984; Lambert et al., 1986). The original contention that melanics enjoy a cryptic advantage on the darkened tree trunks that air pollution has created in industrial areas has been questioned on the basis of several factors, including (1) new data on the resting habits of certain moth species (Sargent, 1969, 1985; Mikkola, 1979), (2) instances of rural melanism, particularly in North America (Klots, 1964, 1966, 1968a, b; Sargent, 1971, 1974, 1983; West, 1977; Manley, 1981), (3) re-assessments of the original mark-release-recapture experiments (Kettlewell, 1955, 1956) that provide the primary evidence for the traditional interpretation (Sermonti and Catastini, 1984), and (4) more general theoretical questions as to the adequacy of the available data to either establish the "classical" case or falsify various alternatives (Hailman, 1982; Lambert et al., 1986).

In light of this increasing skepticism regarding the role of crypsis in promoting melanism in moths, it seems appropriate to look for, and rule out where possible, any other differences between the morphs that might conceivably contribute to the "industrial melanism" phenomenon. Toward that end, I here attempt to determine whether there is an acceptability difference between the typical and melanic morphs of one species that has exhibited increased melanism in recent years.

Fig. 1. The typical (above) and melanic (below) morphs of *P. pallescens* McDunnough. Specimens from Leverett, Massachusetts, 1981. Approximately 2 × life-size.

It seems possible that an acceptability difference between typical and melanic individuals might exist, based either on chemical differences between the morphs (e.g., in melanin content) that could affect their palatabilities, or on different associations that predators might make between each morph and other prey items that they encounter (e.g., typical coloration with palatability, black coloration with unpalatability). Such differences could then play a role in changing the incidence of melanism in natural populations, assuming changes in the composition of the predator and/or prey populations with which the moth species in question was associated.

## METHODS AND MATERIALS

*Panthea pallescens* McDunnough (referred to as *P. furcilla* (Packard) in the prior papers of Ginevan, Jones, Klots, and Sargent) is bivoltine in Massachusetts with adults flying primarily in June and August. The melanic morph, "atrescens" McDunnough (1942), has increased in abundance in recent years (Klots, 1964, 1966, 1968b; Ginevan, 1971; Sargent, 1974; Jones, 1977) and presently comprises ap-

Fig. 2. The experimental feeding dish on the feeding tray at the study site in Leverett, Massachusetts. A white-breasted nuthatch is seen taking a moth.

proximately 60% of the population in the study area. The two morphs of this species are easily distinguished—the typicals having pale gray forewings with prominent black lines, and the melanics having black forewings, with the black lines at least partially edged with white (Fig. 1). I am not aware of any published reports on the resting habits of these moths, but Tobin K. Jones (pers. comm.) has found adults of both morphs resting on trunks of the normal hostplant, white pine (*Pinus strobus* L.).

The specimens were taken at 150-watt incandescent spotlights (Westinghouse outdoor projector) at my home in Leverett, Massachusetts during the collecting seasons of 1982 through 1985. (All of the moths used in this study were collected in this manner, but the butterflies were collected by net during the day, at distances of up to 10 km from my home.) All specimens were immediately frozen in small jars in the freezer compartment of a household refrigerator and were thawed just prior to their use in the bird-feeding trials.

A bird-feeding trial consisted of a 15-min presentation of six thawed Lepidoptera arranged in a circle on a 15.24 cm diameter light blue dish. In every instance, the six specimens represented six different species or distinctive morphs that had been captured within the previous 48 hr. The dish was set out on an open feeding tray (Fig. 2) which was located 1 m from a large glass door through which observations were made. The observer was approximately 2 m from the feeding tray and recorded the specimens taken, in order, and the bird species taking each insect. In addition, other behaviors of the birds were noted when they occurred, as follows: SW = specimen swallowed whole; DWE = specimen taken to perch and there de-winged and eaten; PD = specimen picked up and dropped in place; and TD = specimen taken to perch and dropped. All feeding trials were conducted between 0600 and 0800 hr EDST, and no more than four trials were run on any one day.

Two measures of acceptability for each species (or morph) tested were obtained: the overall percentage of specimens taken, and the average rank of the specimens

Table 1. The numbers and percentages of typical and melanic *P. pallescens* taken by various bird species during feeding trials in Leverett, Massachusetts, 1982–1985.

| Bird species | Typical | | Melanic | |
|---|---|---|---|---|
| | No. | Percent | No. | Percent |
| Blue Jay *Cyanocitta cristata* | 52 | 73.2 | 55 | 73.3 |
| Black-capped Chickadee *Parus atricapillus* | 13 | 18.3 | 17 | 22.7 |
| Tufted Titmouse *Parus bicolor* | 3 | 4.2 | 1 | 1.3 |
| White-breasted Nuthatch *Sitta carolinensis* | 2 | 2.8 | 1 | 1.3 |
| Rufous-sided Towhee *Pipilo erythrophthalmus* | 1 | 1.4 | 1 | 1.3 |
| Totals | 71 | | 75 | |

taken. These two measures were highly correlated (Pearson's correlation coefficient: $r = -0.435$, $P < 0.001$ for the 156 species tested on at least two occasions, $r = -0.699$, $P < 0.0001$ for the 69 species tested on more than 10 occasions), indicating that preferred species were both taken more often and taken earlier in the trials than were less preferred species.

These two measures of acceptability were then utilized to develop a ten-category classification of all of the species (or morphs) that were tested in the feeding trials—these categories ranging from most acceptable (category 1) to least acceptable (category 10) to birds. The percentage of specimens taken and the average rank of the specimens taken were scored as follows:

| Percent taken | Score | Average rank | Score |
|---|---|---|---|
| 80–100 | 1 | 1–1.9 | 1 |
| 60–79 | 2 | 2–2.9 | 2 |
| 40–59 | 3 | 3–3.9 | 3 |
| 20–39 | 4 | 4–4.9 | 4 |
| 0–19 | 5 | 5–6 | 5 |

Table 2. The behavioral responses of birds to typical and melanic specimens of *P. pallescens* during feeding trials in Leverett, Massachusetts, 1982–1985.

| Behaviors | No. of observations (%) | |
|---|---|---|
| | Typical | Melanic |
| Flew off with moth | 55 (76.4) | 62 (79.5) |
| Swallowed moth whole | 15 (20.8) | 11 (14.1) |
| De-winged and ate moth | 1 (1.4) | 2 (2.6) |
| Did not touch | 1 (1.4) | 3 (3.8) |
| Totals | 72 | 78 |

Table 3. The numbers and percentages of typical and melanic *P. pallescens* taken by rank during feeding trials in Leverett, Massachusetts, 1982–1985.

| | Typical | | Melanic | |
|---|---|---|---|---|
| Ranks | No. | Percent | No. | Percent |
| 1 | 24 | 33.8 | 15 | 20.0 |
| 2 | 20 | 28.2 | 21 | 28.0 |
| 3 | 16 | 22.5 | 20 | 26.7 |
| 4 | 5 | 7.0 | 11 | 14.7 |
| 5 | 5 | 7.0 | 6 | 8.0 |
| 6 | 1 | 1.4 | 2 | 2.7 |
| Totals | 71 | | 75 | |

An overall score was obtained by averaging the scores obtained from the percent taken and average rank values. In this way, nine acceptability categories were created with scores ranging from 1, in 0.5 step increments, to 5. In addition, a category 10 was established for those species that were never taken by the birds.

Chi-square goodness-of-fit and contingency tests (Siegel, 1956) were used in analyzing the data.

## RESULTS

Overall, 71 out of 72 typicals (98.6%) and 75 out of 78 melanics (96.2%) were taken by birds ($P > 0.30$) (Fig. 3). The numbers of specimens taken by the different bird species visiting the feeder were virtually identical for the two morphs (Table 1), as were the observed behavioral responses of these birds to the moths (Table 2). No specimen of either morph was picked up and dropped (PD) or taken and dropped (TD) by the birds.

The average rank of the typicals taken was 2.30, and the average rank of the

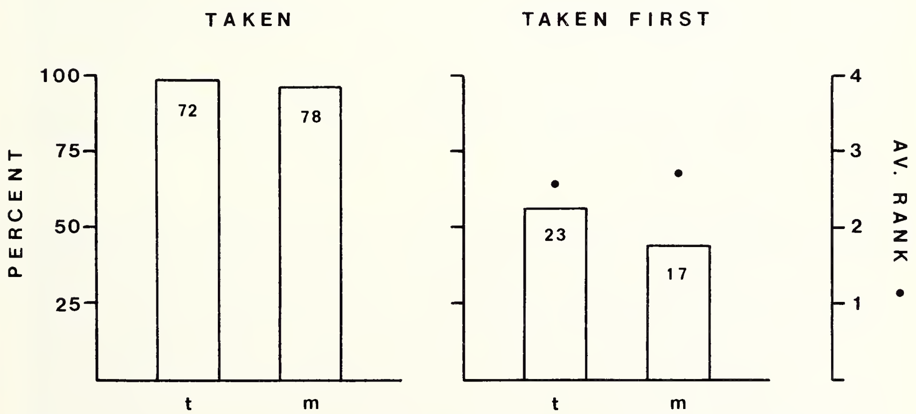


Fig. 3. The percentages of typical and melanic *P. pallescens* taken overall (left) and taken first when paired (right), and the average ranks of typicals and melanics overall (dots). Numbers of individuals are given within the bars; t = typicals, m = melanics.

Table 4. Representative species from the 10 acceptability categories used in the present study.

| Category (no. species) | Species (family) | N | % taken | Av. rank |
|---|---|---|---|---|
| 1 (15) | *Ceratomia undulosa* (Walker) (Sphingidae) | 15 | 100.0 | 1.5 |
| | *Euparthenos nubilis* (Hübner) (Noctuidae) | 10 | 100.0 | 1.6 |
| | *Acronicta americana* (Harris) (Noctuidae) | 45 | 100.0 | 1.7 |
| | *Agrotis ipsilon* (Hufnagel) (Noctuidae) | 14 | 100.0 | 1.9 |
| 2 (35) | *Malacosoma americanum* (F.) (Lasiocampidae) | 46 | 93.5 | 2.6 |
| | *Peridea ferruginea* (Packard) (Notodontidae) | 20 | 95.0 | 2.7 |
| | *Pyrrharctia isabella* (J. E. Smith) (Arctiidae) | 47 | 93.6 | 2.6 |
| | *Catocala amica* (Hübner) (Noctuidae) | 30 | 93.3 | 2.8 |
| | *Charadra deridens* (Guenée) (Noctuidae) | 35 | 97.1 | 2.7 |
| 3 (41) | *Cercyonis pegala* (F.) (Satyridae) | 23 | 73.9 | 2.9 |
| | *Prochoerodes transversata* (Drury) (Geometridae) | 37 | 89.2 | 3.2 |
| | *Dryocampa rubicunda* (F.) (Saturniidae) | 56 | 83.9 | 3.2 |
| | *Spilosoma congrua* Walker (Arctiidae) | 34 | 91.2 | 3.4 |
| | *Lymantria dispar* ♂ (L.) (Lymantriidae) | 51 | 84.3 | 3.1 |
| 4 (18) | *Epargyreus clarus* (Cramer) (Hesperiidae) | 15 | 73.3 | 3.6 |
| | *Malacosoma disstria* Hübner (Lasiocampidae) | 13 | 100.0 | 4.2 |
| | *Parallelia bistriaris* Hübner (Noctuidae) | 42 | 78.6 | 3.4 |
| 5 (20) | *Papilio troilus* L. (Papilionidae) | 18 | 66.7 | 4.4 |
| | *Colias eurytheme* Boisduval (Pieridae) | 19 | 73.7 | 4.5 |
| | *Basilarchia archippus* (Cramer) (Nymphalidae) | 29 | 51.7 | 3.5 |
| | *Xanthotype sospeta* (Drury) (Geometridae) | 17 | 70.6 | 4.6 |
| 6 (16) | *Papilio glaucus* L. (Papilionidae) | 19 | 36.8 | 3.4 |
| | *Artogeia rapae* (L.) (Pieridae) | 43 | 46.5 | 4.3 |

Table 4. Continued.

| Category (no. species) | Species (family) | N | % taken | Av. rank |
|---|---|---|---|---|
| | *Desmia funeralis* (Hübner) (Pyralidae) | 11 | 27.3 | 3.3 |
| | *Campaea perlata* (Guenée) (Geometridae) | 41 | 53.7 | 4.1 |
| 7 (4) | *Danaus plexippus* (L.) (Danaidae) | 17 | 35.3 | 4.2 |
| | *Euchlaena irraria* (Barnes and McDunnough) (Geometridae) | 11 | 54.5 | 5.3 |
| 8 (4) | *Phyciodes tharos* (Drury) (Nymphalidae) | 11 | 27.3 | 5.7 |
| | *Drepana arcuata* Walker (Drepanidae) | 10 | 20.0 | 5.0 |
| 9 (2) | *Itame pustularia* (Guenée) (Geometridae) | 6 | 16.7 | 5.0 |
| | *Haploa lecontei* (Guérin-Meneville) (Arctiidae) | 17 | 11.8 | 5.0 |
| 10 (8) | *Hypoprepia fucosa* Hübner (Arctiidae) | 19 | 0.0 | — |
| | *Cisseps fulvicollis* (Hübner) (Arctiidae) | 8 | 0.0 | — |

melanics taken was 2.71 (Fig. 3). The distributions of ranks for the two morphs (Table 3) were not significantly different ($P > 0.30$).

On the basis of percent taken and average rank, both morphs were assigned to category 2 in the ten-category classification of acceptabilities previously described. For comparison, Table 4 lists a representative array of butterflies and moths ranging from category 1 to category 10 that were also tested in the present study. Both morphs of *P. pallescens* rated slightly above the average for all noctuids tested (887 individuals of 88 species, 93.5% taken, average rank 2.73, average category 2).

Finally, on 40 occasions both morphs were presented to the birds in the same feeding trial. In these cases, the typical was taken first 23 times (57.5%) and the melanic was taken first 17 times (42.5%) ($P > 0.30$) (Fig. 3).

## DISCUSSION

The data presented here indicate that both the typical and melanic morphs of *P. pallescens* are highly acceptable to avian predators. There were no significant differences between the morphs in terms of (1) the numbers of individuals taken, (2) the ranks at which they were taken, (3) the bird species taking them, and (4) the behavioral reactions of the birds to them. In addition, there was no significant difference in the likelihood of either morph being taken first when typicals and melanics were paired in the same feeding trials. Thus, the general conclusion would be that there are no differences in acceptability between the typical and melanic morphs of this species to typical avian predators of the sort they face in nature.

There are hints, however, that the matter cannot be entirely laid to rest. For one thing, melanics fared less well than typicals in every measure used, albeit never significantly so. Thus, fewer melanics were taken overall, they ranked lower than typicals on average, they were less often swallowed whole, and were less likely to be taken first when paired with typicals. This agreement in the direction of difference between the morphs in every measure used is itself improbable, if the morphs are indeed equally acceptable to birds. Thus, while a large difference in acceptability seems safely ruled out by the present data, one cannot rule out the possibility that melanics are slightly less acceptable than typicals.

The question that arises here is the familiar one involving the meaning of statistical significance, or insignificance, in an evolutionary context. If, for example, melanics were not eaten once in every 100 encounters with predators, but typicals were always eaten when encountered, one could not detect this difference (at $P < 0.05$) until one had witnessed nearly 400 instances of each type of encounter. Yet this difference, though smaller than that found between typicals and melanics in the present study, would provide a selective advantage that could ultimately lead to the total replacement of typicals by melanics in a natural population (Fisher, 1930; Falconer, 1960; Dobzhansky, 1970). [Replacement in this case would be relatively rapid, given the simple dominance of the melanic condition (Ginevan, 1971).]

In the present study there was 2.4% difference between the morphs in terms of individuals taken. This difference was insignificant, given the present sample size; but would be significant at $P < 0.05$, if a sample size four times larger than the present one had been obtained. Similarly, the difference between the morphs in the distribution of ranks that was obtained (Table 3) would be significant at $P < 0.05$, if the sample size were doubled.

Thus, a decision as to whether the differences between typicals and melanics reported here represent (1) sampling errors that are to be expected when two sets of individuals are drawn from a single population, or (2) a small, but potentially important, difference in the acceptability of the two morphs, must await the acquisition of additional data.

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